Mechanisms promoting tree species co-existence: Experimental evidence with saplings of subtropical forest ecosystems of China

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Abstract: Questions: The maintainence of a diverse sapling pool is of particular importance for the regeneration and persistance of species-rich forest ecosystems. However, the mechanisms of coexistence of saplings have rarely been studied experimentally. We thus ask: Do species richness, species composition, species identity and stand density have effects on the coexistence, growth patterns and crown architecture of tree saplings? Location: Jiangxi Province, Southeast China Methods: In a field experiment, we manipulated the local neighbourhood of saplings of the four earlysuccessional subtropical species (Schima superba, Elaeocarpus decipiens, Quercus serrata and Castanea henryi) with regard to species richness (1, 2 and 4 species), species composition (monocultures, six two-species combinations and one four-species combination) and stand density (low, intermediate and high). We tested for treatment effects and the impact of species identity on growth variables, biomass allocation, crown architectural traits and branch demography. Results: Species richness was a poor predictor of all response variables, but enhanced pruning and branch turnover. In contrast, species composition proved to be of great importance for growth, biomass allocation, crown architecture and branch demography. Local neighbourhood interactions of saplings were characterised by complementary or facilitative as well as by competitive mechanisms. Intraspecific competition was higher than interspecific competition for two species (C. henryi, Q. serrata) depending on the respective species combination. To a high degree the competitive ability of species can be explained by species identity. Competition for light likely played a major role in our experiment, as evidenced by the strong response of crown architecture and branch demography to the manipulated predictor variables. Conclusions: Effects of species composition and species identity on growth rates and crown architectural variables of tree saplings point to niche separation as a mechanism of species coexistence, while effects of species richness were not yet prominent at the sapling life stage.

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Experimental evidence with saplings of subtropical forest ecosystems of China

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Abstract

Questions: The maintainence of a diverse sapling pool is of particular importance for the regeneration and persistance of species-rich forest ecosystems. However, the mechanisms of coexistence of saplings have rarely been studied experimentally. We thus ask:

Do species richness, species composition, species identity and stand density have effects on the coexistence, growth patterns and crown architecture of tree saplings?

Location: Jiangxi Province, Southeast China

Methods: In a field experiment, we manipulated the local neighbourhood of saplings of the four early-successional subtropical species (*Schima superba*, *Elaeocarpus decipiens*, *Quercus serrata* and *Castanea henryi*) with regard to species richness (1, 2 and 4 species), species composition (monocultures, six two-species combinations and one four-species combination) and stand density (low, intermediate and high). We tested for treatment effects and the impact of species identity on growth variables, biomass allocation, crown architectural traits and branch demography.

Results: Species richness was a poor predictor of all response variables, but enhanced pruning and branch turnover. In contrast, species composition proved to be of great importance for growth, biomass allocation, crown architecture and branch demography. Local neighbourhood interactions of saplings were characterised by complementary or facilitative as well as by competitive mechanisms. Intraspecific competition was higher than interspecific competition for two species (*C. henryi*, *Q. serrata*) depending on the respective species combination. To a high degree the competitive ability of species can be explained by species identity. Competition for light likely played a major role in our experiment, as evidenced by the strong response of crown architecture and branch demography to the manipulated predictor variables.

Conclusions: Effects of species composition and species identity on growth rates and crown architectural variables of tree saplings point to niche separation as a mechanism of species coexistence, while effects of species richness were not yet prominent at the sapling life stage.

Keywords: biomass allocation, branch demography, complementarity, crown architecture, density, facilitation, niche differentiation, species composition, species identity, species richness

Running head: Mechanisms promoting tree species coexistence

1 Introduction

The question as to which mechanisms maintain and promote species coexistence has increasingly raised interest in the light of biodiversity loss and species extinction (Barot 2004; Hillebrand & Matthiessen 2009). Two theories play a key role in the current discussion on plant species coexistence: neutral theory and niche theory. According to neutral theory, functional equivalence (i.e. co-occurring species do not have to be different in rates of growth, dispersal or speciation), together with stochastic events, is a sufficient explanation for species coexistence (Hubbell 2005; Rosindell et al. 2011). Niche theory, by contrast, implies that coexistence is explained by the interspecific differentiation in response to exploitative competition for environmentally limiting resources (DeClerck et al. 2005; Kraft et al. 2008) or in response to species-specific pathogens (Petermann et al. 2008; more general: Loreau & Hector 2001; Silvertown 2004; Levine & HilleRisLambers 2009). Niche partitioning may occur in space, in time or with regard to the quality of resources. As a result, in species combinations resources may be used in a complementary and more efficient way than in monocultures, and interspecific competition is reduced compared to intraspecific competition (Kahmen et al. 2006).

For trees, the most important above-ground resource is light (Denslow 1987; Canham et al. 1994). Since light harvesting efficiency is significantly affected by biomass allocation to leaves, foliage distribution and branching frequency (Niinemets 2010), the separation in niche space with regard to light harvest should be evidenced by species-specific growth patterns, biomass allocation or plant architecture. In addition to abiotic factors competitive interactions strongly influence individual tree growth. In particular, crown dimensions and architecture are known to respond sensitively to local neighbourhood interactions (Biging & Dobbertin 1992; Getzin et al. 2008; Schröter et al. 2011).

However, to explain the spatial development of crowns in detail, information on single branches of individual trees is needed, since the process of crown expansion depends on the spatial development of branches and branch demography, which in turn is affected by local neighbourhood interactions (Franco 1986; Stoll & Schmid 1998; Sumida et al. 2002).

In this study, we experimentally analyse mechanisms of species coexistence of individual trees at the sapling stage, making use of the local neighbourhood approach (Pretzsch 2009). The maintainence of a diverse sapling pool is important to ensure the regeneration and persistence of species-rich forests (Bruelheide et al. 2011). We refer to tree saplings as young tree individuals that have survived the critical seedling phase and whose local neighbourhood is characterised by strong competition caused by a high density of similar-aged individuals. Important factors of this local neighbourhood which might affect the individual performance of tree saplings are species richness and species composition, species identity, stand density and the size of the tree saplings. The focus on individual tree growth patterns, biomass allocation and architectural traits is particularly promising in woody species, because these species have easily identifiable, large individuals with biomass accumulation in long-lasting structures.

We planted saplings of four early-successional subtropical species in monoculture as well as in two- and four-species combinations. In order to determine whether niche separation is the mechanism that enables the coexistence of these species in an early stage of their life, we tested for species richness, species composition and species identity, as well as for density and initial diameter size effects. Specifically, we tested the following hypotheses:

(H1) Species richness of the local neighbourhood affects the growth and morphology of saplings.

(H2) The species composition of the local neighbourhood affects growth and morphology of saplings.

(H3) The species identity of the target sapling is an important predictor of its growth and morphology.

(H4) Density affects growth and morphology of saplings.

2 Materials and Methods

2.1 Study area and experimental design

Our experiment was set up near Xingangshan, Jiangxi province, South-east China (29° 06’ 33’’ N/ 117° 55’ 24’’ E). The study area is characterised by a subtropical monsoon climate with an average annual precipitation of approximately 2,000 mm and a mean temperature of 15.1 °C. The natural vegetation is a subtropical broad-leaved forest with a dominance in abundance of evergreen species (Bruelheide et al. 2011). Nevertheless, the number of occurring deciduous and evergreen species is almost balanced (Lou & Jin 2000). The subtropical broad-leaved forest ecosystems of South-east China represent a global hotspot of phytodiversity (Barthlott et al. 2005).

The experimental area was a former agricultural field, which was ploughed, harrowed and divided into four blocks prior to setting up the experiment in March 2009. Four highly abundant, early-successional species were chosen for the experiment: *Schima superba* Gardn. et Champ., *Elaeocarpus decipiens* Hemsley (evergreen), *Quercus serrata* Murray and *Castanea henryi* (Skan) Rehd. et Wils. (deciduous) (Yu et al. 2001). We manipulated species richness and species composition of tree saplings on plots of 1 m² size. Three plot-related species richness levels were established: monocultures, two-species combinations and four-species combinations. The four monocultures of each species, all six possible two-species combinations, and one four-species combination made a total of eleven species compositions. In addition to enabling the analysis of species richness effects, the comparison of all possible species combinations also makes it possible to identify the effects of intraspecific versus interspecific competition (Massey et al. 2006) as well as competitive dominance of specific species. Species identity was treated as another predictor variable in the experiment. Finally, the species richness and species composition treatments were fully crossed with a density treatment. The low density treatment comprised only one individual per plot, whereas the experimental plots with high and intermediate density each contained 16 individuals, planted in an array of four by four. Planting distances between saplings in the high and intermediate density treatment were 15 and 25 cm, respectively. The high, intermediate and low densities in this experiment refer to 44,000, 25,000 and

10,000 saplings per ha, respectively. In the nearby Gutianshan Nature Reserve, densities of 16,000 individuals per ha were found in an early successional secondary forest stand (< 20 years; Bruelheide et al. 2011). In the species combinations, each species was represented by the same number of individuals in both the peripheral rows (i.e. 12 individuals) as well as in the center (i.e. four individuals). To avoid edge effects, all analyses were performed using the four central individuals. All treatment combinations were replicated four times, once in each of the four blocks. The total number of plots was 132 (11 species compositions x two densities (high, intermediate) x four blocks + 11 low density plots spread over 4 blocks x 4 species = 88 + 44 plots). All treatment combinations were randomly assigned to plots within blocks. The experiment was run until September 2010 when destructive harvest took place. Individuals of the intermediate density treatment of one block were harvested in July 2010.

2.2 Field measurements

Sapling mortality

Over the course of the experiment, 223 out of 1,452 saplings died (15.4 %; number of dead saplings per species: *C. henryi* 92, *S. superba* 95, *Q. serrata* 18, *E. decipiens* 18). Since 96 % of these dead individuals died during the first growing season (March to October 2009), post-planting stress was assumed to be the main reason for sapling mortality. Consequently, only data of saplings that survived this phase of establishment were incorporated in the analyses.

Sapling growth

Total height of saplings (i.e. length from ground to apical meristem) was measured in November 2009 and September 2010. Stem diameter at base height was measured 5 cm above ground in N-S and E-W direction with a caliper, and the mean value was used in the analyses. The position of the diameter measurements was marked permanently with white paint. Measurements were taken in March 2009

(initial stem diameter), November 2009 and September 2010. Growth rates of absolute height and diameter were calculated as: (value (September 2010) - value (November 2009))/ 11.

Above-ground biomass

To analyse biomass allocation patterns with regard to stratification (i.e. height layers) and to different constituents (stem, branches and leaves), the four central individuals per plot were harvested in September 2010 in 50 cm strata starting from ground. Saplings were divided into stem, branches and leaves for each stratum. Biomass was dried at 70° C for 48 h and weighed to 0.01 g precision. Biomass data were logarithmically transformed prior to analyses.

To analyse the vertical above-ground biomass distribution, we calculated the cumulative biomass fraction *C*, i.e. the proportion of cumulative above-ground biomass, summed up from the ground to the height strata *hs* (50, 100, 150, 200, 250 cm). For each individual we fitted the coefficient of vertical biomass distribution as the linear regression coefficient β of *C* over *hs* (see Jackson et al. 1996; Vonlanthen et al. 2010). The coefficient of vertical biomass distribution indicates the steepness of declining *C* with increasing *hs*. Higher coefficient values, in turn, indicate biomass more evenly distributed over the total height of the tree.

Crown architecture

All crown architectural parameters were determined in June and September 2010. A branch was defined as a primary furcation longer than 1 cm. The height of the first branch was measured, and crown length was calculated as the difference between total sapling height and height of the first branch. The length of the first and the longest branch was measured as the distance from the stem to the longest tip of the respective branch.

Branch demography

Branches were counted bi-monthly during winter 2009/10 (November, January, March) and monthly from April to June 2010 and in September 2010. Branch turnover and pruning are interpreted as a measure of adaption ability to changes in neighbourhood conditions over time. Branch turnover was calculated as the sum of all changes in branch number (no matter whether positive or negative) from November 2009 to June 2010. Pruning was defined as the sum of all negative changes in branch number (November 2009 to June 2010) and describes the dieoff of branches over time.

2.3 Statistical analyses

The overall aim of this study was to disentangle neighbourhood effects on growth, biomass allocation, crown architecture and branch demography of saplings. Firstly, the complete dataset was used to test for (H1) by fitting mixed effects models (Model 1) including species richness and density as factorial variables and the initial diameter as fixed effect. The initial diameter was used to account for differences in size at the beginning of the experiment. Secondly, all two species combinations were analysed for species composition (H2). Mixed effects models (Model 2a) were fitted using species composition, density and initial diameter as fixed effects. The analyses with Model 2b were performed for the high density treatment data divided by species to exclude density effects and to test for composition effects on the individual-level of each species. Species composition in Model 2a refered to the mean over all individuals of a given species composition, whereas in Model 2b species composition refered to the mean of individuals of a specific species within a given species composition. Model 2b contained species composition and initial diameter as fixed effects. Thirdly, mixed effects models (Model 3) for all monocultures were calculated to test (H3). They were fitted by the predictor variables species identity, density and initial diameter as fixed effects.

Random effects for all models were plot nested in block. Model simplification was performed by stepwise backward selection of fixed factors, removing the least significant variables until only significant predictory variables remained ($p < 0.05$). Since all density treatments were included in the analyses of Models 1, 2a and 3, the complete data from the June 2010 measurements was used to

ensure a balanced data set. Model residuals did not show violation of modelling assumptions (normality and homogeneity of variances). The significant categorical variables were further examined by a Tukey post-hoc test. For the sake of clarity and more comprehensive analyses, the models presented here did not account for the presence and absence of species (for these models see supporting information S1). We conducted a test for a phylogenetic signal (K statistics) in the observed growth and crown architectural traits. Although the K values for crown length and branch biomass were close to one, none of the values was significant, and we did not consider phylogeny in the statistical analyses (see supporting information S2).

In addition, we calculated Pearson correlation coefficients between height and diameter growth rates and crown architectural variables. If not indicated otherwise, values are given as mean with standard deviation.

All statistical analyses were performed using R 2.12. (R Development Core Team, 2010) using the packages "nlme" for the analyses of mixed effects models (Pinheiro et al. 2010), "multcomp" for post-hoc Tukey tests (Hothorn et al. 2008) and "picante" for the K statistics (Kembel et al. 2010).

3 Results

3.1 Height and diameter increment

The mean sapling height at the time of planting was 33 cm ± 13 cm, compared to a mean height of 124 cm ± 39 cm at the end of the experiment. *S. superba* (6.74 ± 2.17 cm month^{-1}) had the highest mean absolute height growth rate, followed by *E. decipiens* (6.31 ± 2.27 cm month^{-1}), *Q. serrata* (5.57 ± 2.34 cm month^{-1}) and *C. henryi* (3.63 ± 2.67 cm month^{-1}). Species richness had no significant impact on the absolute growth rate of sapling height. However, species composition significantly affected absolute growth rates ($p = 0.03$). Model 2b revealed that the height growth rate of *C. henryi* ($p = 0.019$) and *Q. serrata* ($p = 0.046$) individuals was affected by species composition. Individuals of both species were significantly higher in combination with *E. decipiens* compared to monocultures. The absolute height

growth rate was also influenced by species identity ($p < 0.001$). Neither density nor the initial stem diameter of saplings affected height growth.

The mean absolute growth rates of diameter per month were: *E. decipiens* (0.7 mm ± 0.5) > *S. superba* (0.6 mm ± 0.3) > *Q. serrata* (0.5 mm ± 0.3) > *C. henryi* (0.3 mm ± 0.3). Absolute diameter growth rates were neither affected by species richness nor by species composition. However, species identity was a highly significant predictor of diameter growth ($p = 0.008$). The diameter growth rate of *C. henryi* was significantly lower than that of *S. superba* and *E. decipiens* ($p < 0.05$). In addition, density had a significant influence on absolute diameter growth rate ($p < 0.001$). The diameter growth of saplings was significantly enhanced in the low density treatment compared to both the intermediate and high density treatment ($p < 0.001$). In contrast, the initial stem diameter had no significant effect on diameter growth.

Both absolute height and diameter growth rates were positively correlated with crown length (Pearson correlation coefficient, $r = 0.84$ / 0.50, respectively), the length of the longest branch ($r = 0.40$ / 0.51) and the number of branches ($r = 0.49$ / 0.45).

3.2 Above-ground biomass

Model 1 revealed no significant effect of species richness on above-ground biomass or on the coefficient of vertical biomass distribution. Species composition, in contrast, significantly influenced biomass increment ($p = 0.009$) and allocation to different constituents ($p < 0.01$). Results of Model 2b showed that *C. henryi* individuals accumulated significantly more biomass in combination with *E. decipiens* than in the monoculture ($p < 0.001$) and in combination with *S. superba* ($p = 0.023$, Fig. 1A). The biomass of leaves of *C. henryi* individuals was significantly lower in monocultures than in combination with *E. decipiens* ($p = 0.005$) or in the four species combination ($p = 0.025$, Fig. 1B). Similar to *C. henryi*, the stem and total biomass of *Q. serrata* individuals was higher in combination with *E. decipiens* than in monoculture ($p < 0.01$) and in combination with *C. henryi* ($p < 0.05$, Fig. 1C/ D). Species identity was a significant predictor of all biomass-related variables (all $p < 0.001$). In

general, results of post-hoc Tukey tests revealed that the biomass of all constituents of *C. henyri* was significantly lower than that of the other species (Table 1).

Stratum-related biomass allocation patterns of different constituents proved to be quite stable over density treatments for each species (Fig. 2). Species identity effects were evident for the coefficient of vertical biomass distribution ($p < 0.001$). Increasing density had negative effects on all biomass constituents ($p < 0.05$), whereas no density effects on the vertical biomass distribution were found. Regarding the total above-ground productivity within the low density treatment, the four species ranked as follows: *S. superba* (157.2 ± 134.7 g) > *E. decipiens* (135.2 ± 145.99 g) > *Q. serrata* (97.0 ± 92.3 g) > *C. henryi* (42.0 ± 43.4 g).

3.3 Crown architecture

Species richness had no effect on crown architecture, whereas species composition proved to be a significant predictor for all crown architectural variables ($p < 0.05$ for all variabels). Model 2b results show that species composition had a significant effect on crown length of *C. henryi* and *Q. serrata* and on the length of the longest branch of *S. superba*. The crown length of *C. henryi* was significantly enhanced when growing with *E. decipiens* compared to both the monoculture and the combinations *C. henryi – S. superba* and *C. henryi – Q. serrata* ($p < 0.05$). Moreover, the crown length of *C. henryi* was higher in the four-species combination compared to the monoculture ($p < 0.05$). The crown length of *Q. serrata* was significantly higher when grown with *E. decipiens* compared to the monoculture ($p = 0.008$) and the *Q. serrata – C. henryi* combination ($p = 0.020$). In addition, the crown length of *Q. serrata* was enhanced in the four-species combination compared to the *Q. serrata* monoculture ($p = 0.028$) and combination with *C. henryi* ($p = 0.042$). The length of the longest branch of *S. superba* was significantly enhanced when grown in combination with *C. henryi* compared to the monocultures, the combinations *S. superba – E. decipiens* and *S. superba – Q. serrata,* and the four-species combination (all $p < 0.05$).

3.4 Branch demography

Species richness had no effect on the number of branches (developed at the end of the experiment) but influenced branch turnover ($p = 0.043$) and pruning ($p < 0.001$; Fig. 3). Branch turnover was significantly enhanced in the four species combination compared to the two species combination ($p = 0.047$). Pruning was higher in the four species combinations than in the two species combinations and monocultures ($p < 0.001$). Species composition significantly affected the number of branches, branch turnover and pruning. Species identity significantly affected branch demography (all variables; Table 2).

4. Discussion

4.1 Effects of species richness

Our study analysed for the first time species richness effects on the branch demography of tree saplings. The increase in pruning and branch turnover with higher species number proved the high dynamics in the four species combinations. Sapling individuals may adapt their crown architecture to changes in their local neighbourhood by modifying their branching arrangement (Sumida et al. 2002). These changes may be caused by the species-specific crown architecture of neighbouring saplings and differences in leaf occurence. We interpret the observed highly dynamic branch demography as an effect of proceeding niche differentiation with regard to light harvesting in this relatively complex neighbourhood of the four species combination.

Contrary to our expectations, we found no significant effect of species richness on the other growth and crown architectural parameters. This finding may be attributable to two factors. Firstly, it is well conceivable that diversity effects may evolve at a later stage of sapling development. Lang et al. (2010) analysed older tree individuals (20 – 100 years) of an overlapping species pool (*S. superba*, *Castanopsis eyrei* Champ. ex Benth., *Q. serrata*, *C. henryi*) in the same study region. The authors found that crown area was affected by functional diversity. They concluded that this was due to niche

separation in terms of height stratification, timing of leaf occurrence and crown density (Lang et al. 2010). Secondly, species richness effects on tree growth responses (for example attributable to niche complementarity) might only become apparent at higher levels of diversity (Papaik & Canham 2006). The occupied niche space should increase with higher species number and thereby make niche complementarity more likely to occur.

4.2 Effects of species composition

The effects of species composition on growth, biomass allocation, crown architectural and branch demographic variables indicated that the species identity of neighbouring saplings is an important determinant of sapling growth (H2) in our experiment. This finding is in accordance with studies that demonstrate the importance of neighbour tree identity for growth (e.g. Massey et al. 2006; von Oheimb et al. 2011) and crown formation (Frech et al. 2003; Massey et al. 2006; Lintunen & Kaitaniemi 2010) of individual trees.

We hypothesise that several mechanisms - depending on the species involved - determine effects caused by species composition. These are evidenced by differences in the growth performance of less productive species (here: *C. henryi*, *Q. serrata*; deciduous) in the monocultures compared to combinations containing both highly productive (here: *E. decipiens*, *S. superba*; evergreen) and less productive species.

When growing together with *E. decipiens*, the two species *Q. serrata* and *C. henryi* grew taller and produced more biomass than when growing in monoculture or with other species. These results indicate that intraspecific competition of *C. henryi* and *Q. serrata* individuals was higher than the species' interspecific competition with *E. decipiens*. Massey et al. (2006) also demonstrated that height growth of saplings may increase in heterospecific plots. However, due to a higher branching of the saplings within homospecific plots, the authors did not detect any effect of species composition on above-ground biomass. In our study, the reduced competition experienced by *C. henryi* and *Q. serrata* was caused to a greater extent by the species identity of the competitor, i.e. by *E. decipiens*, than by the

fact that it was growing with any heterospecific neighbour. Based on the observed high productivity of *E. decipiens* in the low density treatment, we would have expected a reduced performance of less competitive species in combinations with *E. decipiens*. In addition, the biomass of *E. decipiens* individuals was not affected by species composition. Thus, the increased growth of *C. henryi* and *Q. serrata* in combination with *E. decipiens* indicate the existence of complementary or facilitative mechanisms.

The enhanced crown length of *C. henryi* and *Q. serrata* in combinations with *E. decipiens* points to complementarity of crown architecture. Complementary effects and, thus, reduced interspecific competition for light within the four-species plots compared to high intraspecific competition in monocultures also resulted in longer crowns in both species. In contrast, *C. henryi* had shorter crowns in combination with *S. superba,* than in combination with *E. decipiens*. This indicates - together with the enhanced length of the longest branch of *S. superba* in combination with *C. henryi* - negative competitive effects of *S. superba.* The effects of species composition on crown architectural variables highlight the importance of competition for light as a structuring factor of neighbourhood interactions.

4.3 Effects of species identity

Species identity was a strong predictor throughout the whole experiment. We found all the response variables analysed to be affected by species identity, which confirms our H3. Our findings approve the results of other studies that described species-specific relative growth rates (Dekker et al. 2008; Suter et al. 2010) and crown architecture (Takyu 1998). Branching frequency, foliage distribution, and biomass allocation to leaves significantly affect light harvesting (Niinemets 2010). Energy gain by increased light harvesting is likely to be converted to growth, and thus, sapling growth and survival was found to be related to architectural traits (Takyu 1998; Sterck et al. 2003; Dekker et al. 2008). In our study, height and diameter growth were also found to be related to the vertical and horizontal crown dimensions.

When ranking the observed species according to their productivity, the two evergreens performed better than the two deciduous species. In contrast to our results, seedlings (< 0.5 yrs) of evergreen species in the same study region have been found to accumulate less biomass and to show a reduced phenotypic plasticity with regard to shade than deciduous species in a greenhouse experiment (Böhnke & Bruelheide 2011). However, the saplings in our experiment were older, and, thus, effects of their growth performance during the seedling stage were of minor importance. The advantages of evergreen leaves, i.e. longer photosynthetic season, lower costs of replacing leaf nutrients and tougher laminae to endure frost, drought and herbivory (Givnish 2002), might also have contributed to the better performance of the evergreen species in our experiment.

Our results indicated a close relationship between species identity and branch demography. Species identity effects on branch demography were pronounced, since each of the four species had a different branch development strategy. The number of branches was low for *C. henryi* and *S. superba*. Whereas *S. superba* had the lowest degree of pruning and thus was able to invest more in stem biomass, *C. henryi* displayed high branch mortality, combined with long branches and smaller height increments. In contrast, *Q. serrata* had an intermediate number of branches and degree of pruning. High turnover rates and branch numbers of *E. decipiens* combined with large height and diameter growth suggest that this species may be able to adapt quickly to changes in the local light environment and, thus, to optimize its foraging for light by means of a highly flexible biomass allocation to branches. The differences between species in branch demography may be seen as niche separation with regard to light harvesting. Furthermore, different branch demography results in distinct crown architecture of spalings which has important effects on ecosystem functions such as the reduction of erosive power of rain throughfall (Geißler et al. 2012).

4.4 Effects of density

We found a negative effect of density on diameter growth rates but no density effects on height growth, thus partly confirming H4. Our findings are in agreement with competition studies, according

to which diameter growth was often found to be influenced by the local neighbourhood (Biging & Dobbertin 1992; Canham et al. 2004; von Oheimb et al. 2011). The significant reduction of biomass in all constituents of saplings of the high density plots indicated that competition increased with increasing stand density.

In addition, density significantly affected crown architecture. A positive effect of reduced stand density on crown area was found for mature trees by Yu et al. (2003) and Hein et al. (2008). However, while the number and length of branches of loblolly pine increased with decreased density (Yu et al. 2003) this was not the case in Douglas fir (Hein et al. 2008). Thus, effects of density on crown architecture might be species-specific and generally depend on the distances to the neighbours which a tree individual may encounter in a respective stand.

Conclusions were deleted

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Tables:

Table 1. Mean values of above-ground biomass allocation to different constituents (dry weight per plant [g] and standard deviations) for the four species. Different letters show significant post-hoc Tukey results.

Constituents	*C. henryi*	*E. decipiens*	*Q. serrata*	*S. superba*
Total	13.9 ± 10.8 [a]	34.5 ± 33.6 [b]	37.8 ± 25.6 [b]	56.7 ± 33.7 [b]
Stem	20.2 ± 22.8 [a]	69.9 ± 68.6 [b]	47.9 ± 45.8 [b]	57.3 ± 42.8 [b]
Branches	13.6 ± 14.6 [a]	44.7 ± 62.2 [b]	18.5 ± 22.2 [a]	32.5 ± 36.3 [b]
Leaves	8.2 ± 11.0 [a]	20.6 ± 30.3 [ab]	30.1 ± 28.0 [b]	67.4 ± 61.9 [c]

Table 2. Crown architecture and branch demography. Values are means for species and density treatments. Different letters show significant differences of post-hoc Tukey tests.

Crown characteristic	Species means				Density means		
	C. henryi	*E. decipiens*	*Q. serrata*	*S. superba*	Low	Middle	Dense
Height of first branch [cm]	8.94	6.17	13.36	13.15	4.52 [a]	9.85 [ab]	10.91 [b]
Crown length [cm]	72.89	106.15	76.02	80.97	94.76	89.78	82.08
Length of first branch [cm]	38.91 [a]	21.64 [b]	24.42 [b]	36.24 [a]	26.05 [ab]	36.16 [b]	24.12 [a]
Length of longest branch [cm]	52.65	62.14	43.85	52.82	65.05 [b]	58.01 [b]	48.13 [a]
Number of branches #	6.89 [a]	21.32 [c]	16.54 [b]	9.56 [a]	17.64 [b]	13.64 [ab]	12.82 [a]
Branch turnover *	15.48 [ab]	30.72 [c]	22.31 [bc]	14.14 [a]	27.12 [b]	22.85 [b]	19.05 [a]
Pruning °	6.23 [a]	6.85 [b]	4.99 [b]	4.16 [b]	6.77	6.01	5.09

All branches exceeding 1 cm in length, counted in June 2010.
* Sum of all changes in branch number (positive and negative) from November 2009 to June 2010.
° Sum of all negative changes in branch number (November 2009 to June 2010).

Fig. 1. Boxplots of the individual total biomass (A) and leaf biomass (B) of *C. henryi,* and of total biomass (C) and stem biomass (D) of *Q. serrata* in the different species compositions. Significances of post-hoc Tukey tests of the explanatory variable "species composition" tested by Models 2b are indicated by different letters. Species codes: Ch: *C. henryi*; Ed: *E. decipiens*; Qs: *Q. serrata*; Ss: *S. superba*.

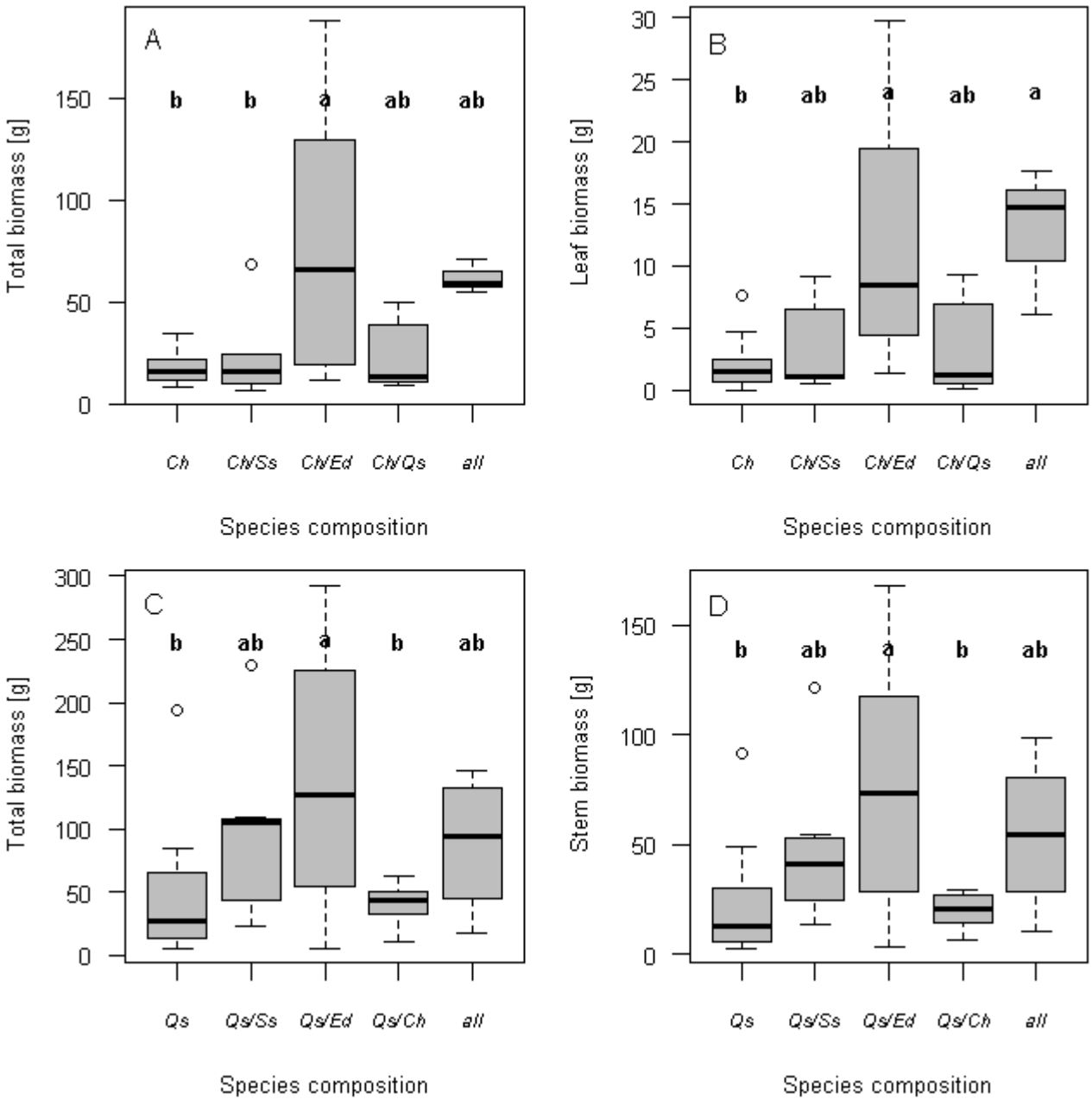


Fig. 2. Allocation patterns of the biomass constituents (stem, branches, leaves) per individual over different strata. Mean biomass values per strata are shown for species of the different density treatments (barplots). Each stratum comprises 50 cm in height. The black line represents the mean coefficient of vertical biomass distribution for the respective species and density treatment.

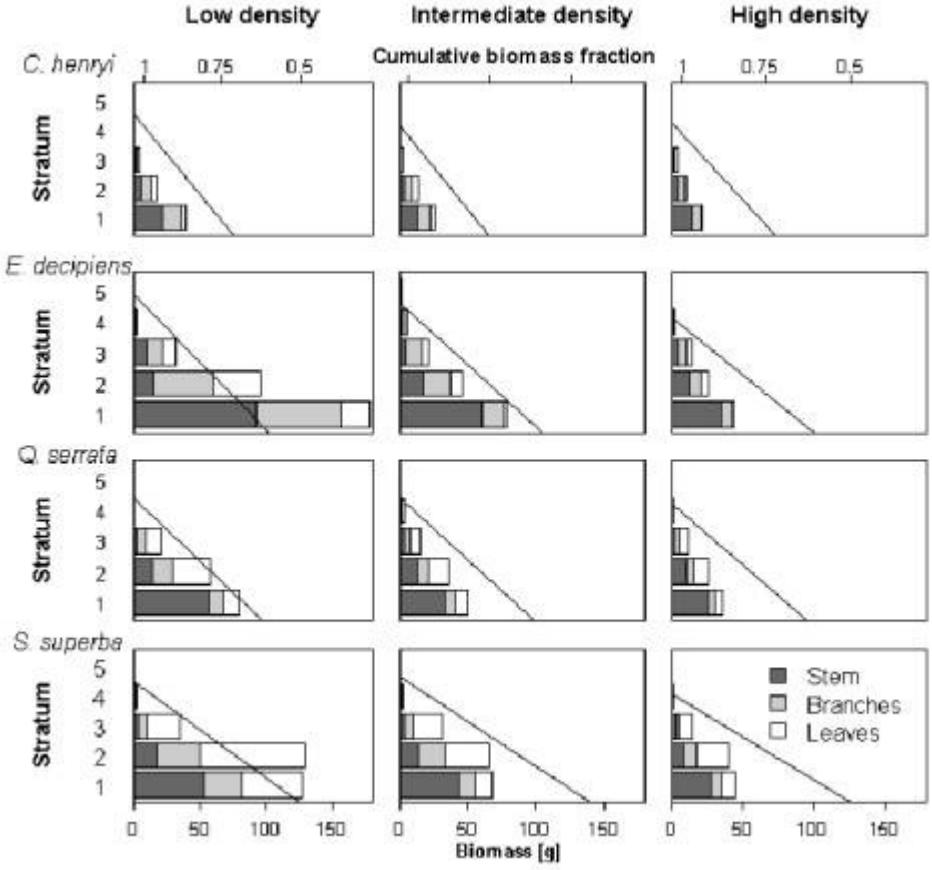
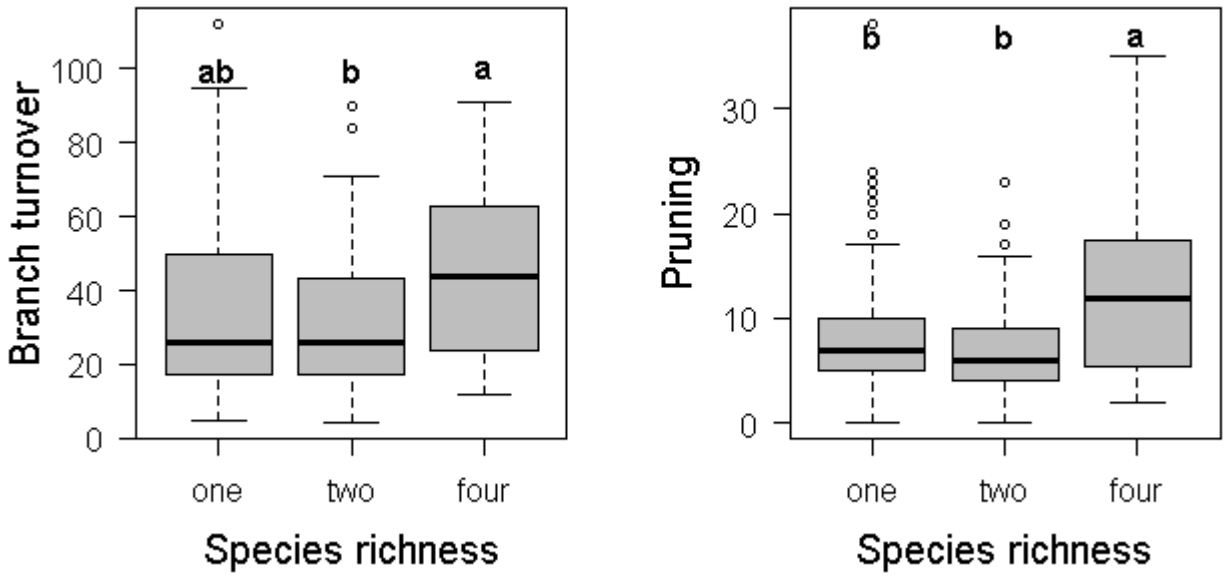


Fig. 3. Boxplots of branch turnover and pruning for species richness levels. Branch turnover is the sum of all positive and negative changes in branch number, whereas pruning is the sum of branch losses over the duration of the experiment. Significances of post-hoc Tukey tests of species richness tested by Model 1 are indicated by different letters.



Supplementary material:

Online Appendix S1: An alternative analysis of our results
Online Appendix S2: Test of phylogenetic signal in the traits

Electronic Appendix S1:

An alternative analysis of our results.

The explanatory variable species richness may be captured as a factorial variable (Sf), as a linear or as a loglinear variable. It may also be represented by a contrast of monocultures versus species combinations (mono). We tested for all these different species richness variables in Models A. In Models B, we tested for the effect of species presence (used as contrast of presence versus absence) and all two-way interactions, and in Models C for the species composition (comp, factorial variable). Due to the experimental design it was not possible to test for all these effects within one model. In addition, full models contained the fixed effects: species identity (ID), density and the initial diameter of the saplings (init dia). Random effects were plot nested in block. Model simplification was performed by stepwise backward selection of fixed factors, removing the least significant variables until only significant predictory variables remained ($p < 0.05$). The table shows results of the most parsimonious models. AIC values are given to compare the goodness of fit of the Models A-C for each response variable. Species names are given as: *Castanea henryi* (CH), *Elaeocarpus decipiens* (ED), *Quercus serrata* (QS), *Schima superba* (SS).

	Absolute growth rate												Biomass					
	Height						Diameter						Total					
Model	A		B		C		A		B		C		A		B		C	
AIC	1214.09		1213.69		**1209.23**		**213.13**		217.16		253.01		735.67		**735.21**		745.30	
	F-value	p	F-value	p	F-value	p	F-value	p	F-value	p	F-value	p	F-value	p	F-value	p	F-value	p
Sf	3.08		-		-		-		-		-		-		-		-	
Comp	-		-		7.71	***	-		-		2.92	**	-		-		8.72	***
CH	-		27.36	***	-		-		14.78	***	-		-		37.00	***	-	
ED	-		8.29	**	-		-		-		-		-		5.56	*	-	
QS	-		-		-		-		-		-		-		0.05		-	
SS	-		10.71	**	-		-		-		-		-		11.83	***	-	
ID	34.46	***	22.12	***	16.68	***	17.68	***	12.68	***	10.21	***	31.78	***	17.46	***	11.79	***
Density	-		-		-		19.33	***	20.69	***	20.62	***	12.57	***	17.31	***	17.59	***
init dia	7.50	**	8.75	**	5.33	*	-		-		-		32.90	***	33.36	***	31.16	***
ED:QS	-		-		-		-		-		-		-		-		-	
ED:SS	-		8.43	**	-		-		-		-		-		16.84	***	-	

	Biomass															
	Stem						Branches						Leaves			
Model	A		B		C		A		B		C		A		B		C	
AIC	2951.39		2908.83		**2883.17**		**773.20**		777.27		786.46		786.58		**785.59**		790.99	
	F-value	p	F-value	p	F-value	p	F-value	p	F-value	p	F-value	p	F-value	p	F-value	p	F-value	p
Sf	-		-		-		-		-		-		-		-		-	
Comp	-		-		4.48	***	-		-		6.32	***	-		-		16.66	***
CH	-		13.41	***	-		-		16.74	***	-		-		71.60	***	-	
ED	-		9.95	**	-		-		14.61	***	-		-		4.06	*	-	
QS	-		0.16		-		-		6.58	*	-		-		-		-	
SS	-		0.08		-		-		1.53		-		-		39.34	***	-	
ID	15.58	***	9.79	***	8.56	***	21.43	***	10.45	***	7.72	***	68.07	***	35.58	***	25.31	***
Density	4.76	**	5.75	**	6.24	**	22.78	***	26.74	***	25.93	***	16.54	***	20.15	***	21.45	***
ini dia	43.34	***	44.62	***	41.50	***	27.22	***	27.44	***	25.28	***	12.02	***	11.54	***	11.60	***
ED:QS	-		5.70	*	-		-		-		-		-		-		-	
ED:SS	-		8.38	**	-		-		12.41	***	-		-		9.30	**	-	

	Biomass					
	Coefficient of vertical biomass distribution					
Model	A		B		C	
AIC	**418.10**		426.11		438.77	
	F-value	p	F-value	p	F-value	p
Sf	-		-		-	
Comp	-		-		3.64	***
CH	-		4.56	*	-	
ED	-		3.26		-	
QS	-		-		-	
SS	-		8.12	**	-	
ID	8.74	***	5.54	**	4.33	**
Density	-		-		-	
init dia	-		-		-	
ED:QS	-		-		-	
ED:SS	-		6.61	*	-	

	Crown architecture															
	Height of first branch						Crown length						Length of first branch			
Model	A		B		C		A		B		C		A		B		C	
AIC	**1321.58**		1321.97		1328.21		3095.30		3066.12		**3040.28**		2939.80		**2922.8**		2898.29	
	F-value	p	F-value	p	F-value	p	F-value	p	F-value	p	F-value	p	F-value	p	F-value	p	F-value	p
Model	4.99	*	-		-		-		-		-		-		-		-	
Sf	-		-		-		-		-		-		-		-		-	
Comp	-		-		2.35	*	-		-		7.40	***	-		-		3.70	***
CH	-		6.61	*	-		-		3.99	*	-		-		14.18	***	-	
ED	-		-		-		-		44.40	***	-		-		5.56	*	-	
QS	-		-		-		-		6.65	*	-		-		6.72	*	-	
SS	-		10.91	*	-		-		5.03	*	-		-		-		-	
ID	7.28	***	3.91	*	4.23	**	26.46	***	9.92	***	10.26	***	15.94	***	7.54	***	6.88	***
Density	6.55	**	8.21	***	6.41	**	4.69	*	5.41	**	5.13	**	3.64	*	3.80	*	3.71	*
init dia	-		-		-		32.59	***	32.02	***	30.69	***	-		-		-	
ED:SS	-		-		-		-		10.43	**	-		-		-		-	
ED:CH	-		-		-		-		-		-		-		7.18	**	-	
CH:ED	-		-		-		-		-		-		-		-		-	
CH:SS	-		-		-		-		-		-		-		-		-	

	Crown architecture						Branch demography									
	Length of longest branch						Number of branches						Branch turnover			
Model	A		B		C		A		B		C		A		B		C	
AIC	2977.40		2972.59		**2937.85**		2239.14		2235.40		**2221.45**		1106.78		**1103.30**		1108.04	
	F-value	p	F-value	p	F-value	p	F-value	p	F-value	p	F-value	p	F-value	p	F-value	p	F-value	p
mono	-		-		-		-		-		-		-		-		-	
Sf	-		-		-		-		-		-		5.76	**	-		-	
Comp	-		-		3.08	**	-		-		14.73	***	-		-		14.26	***
CH	-		-		-		-		37.53	***	-		-		20.70	***	-	
ED	-		10.4701	**	-		-		59.54	***	-		-		87.86	***	-	
QS	-		11.6678	***	-		-		16.22	***	-		-		6.48	*	-	
SS	9.53	***	-		4.41	***	-		20.36	***	-		-		7.01	**	-	
ID	11.72	***	4.42	**	3.83	*	72.01	***	28.65	***	25.48	***	56.28	***	23.00	***	20.92	***
Density	5.67	**	5.59	**	6.09	**	6.81	**	7.58	***	7.26	**	6.85	**	10.42	***	7.07	**
init dia	20.78	***	20.50	***	19.87	***	24.57	***	24.04	***	23.36	***	11.28	***	10.49	**	11.23	**
ED:SS	-		4.23	*	-		-		-		-		-		-		-	
ED:CH	-		1.67		-		-		-		-		-		-		-	
CH:ED	-		5.62	**	-		-		-		-		-		5.91	*	-	
CH:SS	9.67	***	11.22	***	5.44	**	-		-		-		-		6.92	**	-	
	7.13	**	3.54		6.90	**												

Model	Branch demography					
	Pruning					
	A		B		C	
AIC	**836.34**		844.87		851.45	
	F-value	p	F-value	p	F-value	p
mono	-		-		-	
Sf	-		-		-	
Comp	-		0.00		-	
CH	-		17.81	***	-	
ED	-		4.23		-	
QS	-		1.67		-	
SS	-		5.62	**	-	
ID	9.67	***	11.22	***	5.44	**
Density	7.13	**	3.54		6.90	**
init dia	-		-		4.21	*
ED:SS	-		-		-	
ED:CH	-		-		-	
CH:ED	-		-		-	
CH:SS	-		7.48	0	-	

Electronic Appendix S2

Test of phylogenetic signal in the traits

To confirm that the analysed trait data of our four observed species are statistically independent and not influenced by the phylogenetic relatedness of the species, we run a test of phylogenetic signal in the species traits. K statistics were calculated, which describe the strength of phylogenetic signal compared with an expectation based only on the phylogenetic tree topology and branch lengths and assuming Brownian motion character evolution (Blomberg et al. 2003). A K value less than one indicates that the phylogentic signal is less than expected under Brownian motion evolution, whereas a K value greater than one implies a strong phylogenetic signal. The significance of the phylogenetic signal can be tested by comparing the observed patterns of the variance of independent contrasts of the trait to a null model of shuffling taxa labels across the tips of the phylogeny (Kembel 2010). The analyses were done by means of the R-package picante (Kembel et al. 2010).

For the construction of the phylogenetic tree, sequences of rbcL and matK were downloaded from NCBI Genbank (http://www.ncbi.nlm.nih.gov/; Tab 1) for the species of interest or of closest available relatives (for *C. henryi*) and aligned with ClustalW in Bioedit. Based on the combined alignment consisting of 1094 bp a phylogenetic hypothesis was generated using Maximum likelihood (Fig. 1) in MEGA5 (Tamura et al. 2011) applying the Tamura-Nei model of base substitution, uniform mutation rates, complete deletion of gaps and tree inference by nearest-neighbour-interchange. Branch lengths in the ML tree are a direct measure of the number of base substitutions.

Table 1. Accession numbers of sequences used.

	*rbc*L	*mat*K
Castanea henryi	M94936 (*Castanea sativa*)	EF057123
Elaeocarpus decipiens	HQ427154	HQ415261
Quercus serrata	HQ427171	HQ427319
Schima superba	HQ427230	HQ427375

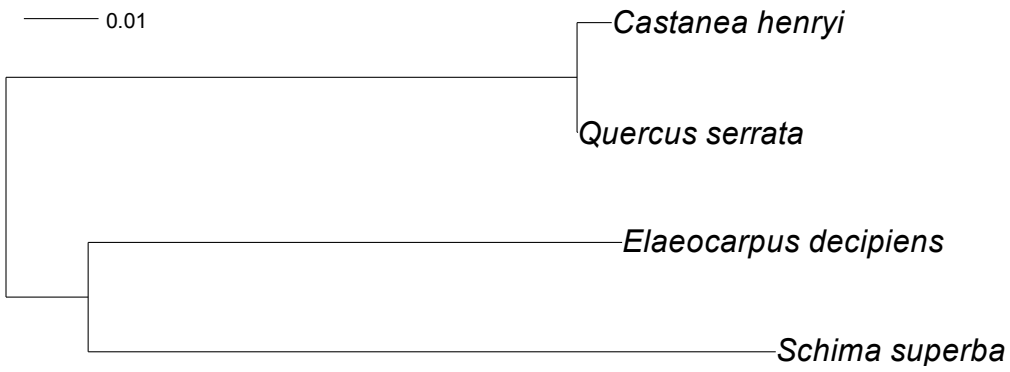


Fig. 1 Maximum Likelihood tree based on combined rbcL and matK sequences.

As indicated in Tab. 2 we could not detect a significant signal of phylogeny in the analysed traits of the present study. Although the K values for crown length and the biomass of branches were close to one, the comparison to the null model revealed no significant effect of phylogeny. Thus, we assumed that our data points were statistically independent and we did not consider phylogenetic structure in the further statistical analyses. However, we are aware that the power to detect phylogenetic signals was found to be low for trees including fewer than 20 taxa (Blomberg et al. 2003).

Table 2. Results of the test of phylogenetic signal in the observed traits.

Trait	K	Observed variance of PICs	Mean variance of PICs of null modell	p-value of PIC variance
Height of first branch	0.11	2299.40	2788.25	0.63
Crown length	1.13	4387.18	50984.34	0.11
Length of first branch	0.08	23106.70	16224.61	0.52
Length of longest branch	0.12	9314.27	12637.06	0.40
Number of branches	0.10	10359.05	9853.72	0.53
Branch turnover	0.23	5817.04	12610.89	0.24
Pruning	0.16	187.85	332.94	0.44
Total biomass	0.11	62621.75	68832.84	0.69
Biomass of stem	0.13	83436.53	97420.59	0.59
Biomass of branches	0.93	4705.89	45150.05	0.07
Biomass of leaves	0.24	58293.25	149750.79	0.36

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